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THE NERVOUS SYSTEM OF THE CESTODE MONEZIA EXPANSA.

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WITH SIX PLATES.

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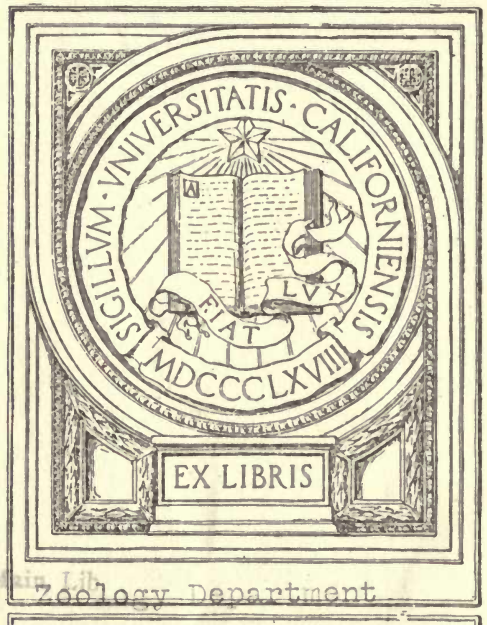

The Nervous System in the Cestode Moniezia expansa.

By

Wm. L. Tower.

With Plates 21—26.

Contents.

Introduction.

The work of which this is an account was done during the winter of 1895—96. A preliminary paper was published in the Zoologischer Anzeiger, July 20, 1896. It was my intention at that time to follow the preliminary paper with a final one as soon as it could be prepared, but ill-heath and other circumstances over which I have had no control have delayed its preparation much longer than I expected.

When this work was begun the knowledge of the nervous system in Cestodes was in a very unsatisfactory condition. The anatomy, and, to some extent, the histology of these forms, exclusive of the nervous system, were fairly well known. Considering the valuable

results obtained by many authors in using the chrome-osmium-silver method of GOLGI and the methylen-blue method in neurological studies on other animals, and the interesting character of these worms, it is rather surprising that the condition of the nervous system should have been incompletely determined. Some explanation of this may be found, however, in the seemingly indifferent action of the chrome-osmium-silver method upon Invertebrates in general; in the transient character of methylen-blue impregnations; in the loose arrangement, the non-medullated character, and the small size of the nerve fibres of Cestodes, which render ordinary stains useless; and in the consequently almost total failure of the best nerve methods when applied to these parasites. All these conditions combine to make the study of the nervous system in Cestodes very difficult.

From the time of NIEMIEC's (1885) paper until that of BLOCHMANN (1895) little or nothing had been discovered on this subject. Previous to the appearance of BLOCHMANN's paper the nervous system of the Taenias had been known to consist of a system of ganglia, commissures, and connectives in the scolex, more or less complex, according to the species, as described by NIEMIEC (1885); one large and one or two accessory lateral nerve trunks, lying external to the longitudinal excretory tube; and two dorsal and two ventral nerves that could not be traced beyond the neck region. Occasional branchings of these nerves in the proglottides had been recorded by various authors, but the course of these branches, and the existence of ganglionic cells had not been clearly demonstrated in any form until within the past two years. The papers of BLOCHMANN, ZERNECKE, LÜHE and COHN, a note by KÖHLER and one by myself all confirm the existence of a constant, definite and extensive system of ganglia, commissures, and connectives, a wealth of ganglionic cells, and the existence of nerve terminations in the periphery of the animal that would seem to indicate for them a sensory function.

These results have been obtained by the use of three methods: that of GOLGI, the methylen-blue intra-vitam stain, and the proper use of VOM RATH's fluid. In my work I have been only slightly successful with methylen-blue, and wholly unsuccessful with GOLGI's method; but by the careful manipulation of the material in VOM RATH's fluid, followed by crude pyroligneous acid, very desirable results have been obtained. Many other methods have been tried, but without success.

Another and rather difficult problem constantly confronted me

during the progress of my study — that of keeping the worms alive and constantly at hand for use in the laboratory. Although material was abundant at the abattoir, it required considerable time and trouble to obtain it, and when working with methylen-blue it was absolutely necessary to have a constant supply of living material. As the methods given by LÖNNBERG for this purpose were a failure, as far as this species was concerned, considerable time was spent in experimenting with different mixtures and methods for keeping the worms alive.

I. Material and Methods.

A. Material.

Abundant material from the small intestine of *Ovis aries* was obtained as needed from the abattoirs of Boston. The cestodes *Moniezia expansa* were taken from the intestines shortly after the animals were slaughtered and before the viscera became cooled. It was found best to visit the abattoir early in the morning soon after work had commenced, as one was then sure of being able to examine the viscera before they became cool, or had suffered from lying in heaps in the "gut room", or from the rough handling which often destroys the larger and more desirable specimens.

In removing the worms it was found undesirable to slit open the intestine, but much better to sever it near the beginning of the coecum, then, beginning at the pylorus, slowly to "strip" the intestine between the thumb and forefinger, causing the contents to flow from the cut end. In parasitized animals the greater number of worms were found in the ilium, or caudal portion of the intestine, a few in the jejunum, and only occasionally one in the duodenal region. Although this method of removing the worms was not all pleasant, it was rapid and practical. Moreover, by this method, the worms could be removed not only in a more satisfactory and less broken condition, but more easily and rapidly, and without exposing them to the air as long as in the process of opening the intestine longitudinally. In almost every case where the worms were removed in this manner the scolex came away with the proglottides. Moreover, the scolex was not injured in any way by this treatment, as the worms evidently relax their hold upon the intestinal wall; whereas, if the intestine was slit open and the worms taken out, they invariably held tightly to the wall, and could be removed only by being pulled or cut away. This resulted

in distorting and often tearing the scolex to such an extent as to render it unfit for use. Each parasitized animal usually contained from two to fifteen worms, each from 50 cm to 200 cm in length, and I have occasionally taken more than fifty (once 58) good-sized worms from one host.

B. Methods.

1. Media for Collection and Transportation.

The worms were quickly separated from the contents of the intestines by the fingers, not with forceps, and placed in one of several media for transportation to the laboratory. For this purpose physiological salt solution (0,75 %) was first used. This was tried at various temperatures, from 10° C to 30° C, but was found to be uniformly harmful, as it produced stupefaction and rapid death, accompanied by a more or less marked plasmolysis. Distilled water, faucet water, and distilled water with sodium chloride in varying percents (1 % to 6,5 %) were in the lower grades accompanied by strong plasmolysis, while the higher percents acted as an irritating stimulant, producing distortions and death. If the material was afterwards to be treated with VOM RATH'S mixture, the physiological salt solution gave fair results, provided the worms were placed in his mixture as soon as the laboratory was reached. It was positively harmful, however, to allow the worms to remain in this solution more than one hour; for, even after only an hours exposure, VOM RATH'S method was rather ineffective, as far as the demonstration of the nerves was concerned. It would have been more desirable to have placed the worms in the killing fluid at the abattoir; but, as all foreign substances had to be removed before killing, and this could not be done at the abattoir, it was necessary to defer the killing until they had been taken to the laboratory.

A mixture produced by adding one percent of pepsin to normal salt solution gave better results, as the reaction upon the worms was not as pronounced as that shown by the physiological salt solution. With material collected in this mixture, as also with that in the simple salt solution, I was unable to obtain a satisfactory intra-vitam stain by the methylen-blue method or a satisfactory GOLGI impregnation, although methylen-blue was found to stain to some extent. If the amount of sodium chloride was decreased and that of pepsin increased to the following proportions,

hydrant water . . . . 100,0 ccm
sodium chloride . . . 0,5 g
pepsin . . . . . 1,5 g

the results were still more satisfactory; but even with material collected in this mixture neither GOLGI impregnations nor methylen-blue stains were obtained. When killed in VOM RATH's mixture material collected in this fluid gave very good results; but the best fluid found for the transportation of the worms contained no sodium chloride. It was composed of

hydrant water . . . . 100 ccm
pepsin . . . . . 2 g
egg albumen (fresh) 10 to 15 g

Worms placed in this mixture appeared to suffer no harm even if left for several hours provided the temperature did not go delow 10° C nor above 30° C. With worms collected in this fluid a fair methylen-blue intra-vitam stain was obtained, but, as my work was nearly at an end before this solution was tried, I have not been able to test it fully.

For all ordinary purposes, preparatory to killing in the more common reagents, I believe the worms could be collected in the physiological salt solution without any appreciable change either in cell arrangement or cell contents; but for the study of nerves the material should not be placed in physiological salt solution, nor in any solution containing sodium chloride.

2. Keeping Cestodes Alive in the Laboratory.

When the laboratory was reached the material was first washed or rinsed in the fluid in which it was collected, or in a fresh supply of the same, until it was free from all dirt and chyme. It was then placed in a fresh, clean portion of the fluid, and finally in from 20 to 30 minutes after being taken from the animal, the worms were ready for the killing reagents.

In many cases it was found desirable to keep the worms alive for a greater or less length of time, especially when the methylen-blue process was employed. Attempts to keep the worms in any mixture containing salt were fruitless, as they could not thus be made to live more than a few hours at most. Distilled water and hydrant water were both equally worthless, but after considerable experimenting and many failures the following mixture was compounded, in which,

with proper care, it was possible to keep the worms alive for 2, 3 or 4, and sometimes even for 5 days:

hydrant water	100 ccm
egg albumen (fresh) . .	10 g
pepsin	2 g
cane sugar	2 g
prepared beef (Bovox). .	5 g

The worms, only one or two in a dish, were placed in this mixture freshly made, of which 100 ccm was allowed to each worm. They were kept in the laboratory in the dark, no attention being paid to temperature, for it was found that the temperature between certain limits (10° C to 30° C) was not a very important factor, although about 17° C seemed to be the most favorable. Every morning the worms were placed in a freshly made mixture, care being taken to clean thoroughly the dishes before the fresh culture-solution was put into them. I was unable to use successfully the methods given by LÖNNBERG (1892) for keeping Cestodes alive in the laboratory.

3. Methods of Fixing and Staining the Nervous Tissues.

The chrome-osmium-silver methods of GOLGI, both the slow and the rapid, with various modifications proposed by recent writers were the ones chiefly tried, but always without success. I was unable to determine the cause of failure. In nearly all cases there was, however, a good impregnatiou of the dorso-ventral, longitudinal, and transverse muscle fibres. The plan proposed by STRONG (1895) of using formic aldehyde in place of osmic acid was also unsuccessful, although this combination gave good results for other Invertebrates (e. g. *Echinorhynchus*), used in check experiments.

Various modifications of the gold-chloride methods were not more successful than the GOLGI methods.

With the axis-cylinder stains the results were likewise unsatisfactory, although better than with the GOLGI and gold-chloride methods. The method of NISSL (1886) gave a good stain of the lateral nerve, and by its use many of the other nerves could be traced after one had learned where to look for them; but this stain did not differentiate nervous tissue from muscular and connective tissue. The method of ALT (1892) was useless for my purpose. REHM's (1892) method was also unsatisfactory in that it did not separate nervous from muscular and connective tissue. WOLTER's method was the most satisfactory for staining the axis cylinder, but it did not dif-

ferentiate nerve tissues from the other tissues as well as VOM RATH's method.

Throughout the most of my work material was used that had been subjected to sodium chloride solutions, but finally the solution described on page 363 was tried and gave good results. Unfortunately the opportunity was wanting for continuing the work with this more favorable material. The method which at the last was found best adapted to *Moniezia* was as follows: The material collected at the abattoir was placed in the solution the formula for which is given on page 363, and was thus carried to the laboratory. It was there washed and the worms not required at once were placed in the culture solution described above (page 364). Those which were to be treated immediately were cut into pieces consisting of two or three proglottides each, dried for a moment on filter paper, and placed in a clean watch glass. The pieces were then covered with a freshly made mixture composed of 60 and 40 volumes respectively of the following solutions, A and B:

A. methylen-blue (dry) . 1 g
hydrant water . . . 1000 ccm
B. egg albumen (fresh) . 60 g
hydrant water . . . 40 ccm

Only enough of this mixture was used to cover the specimens, a little being added from time to time to replace that lost by evaporation. It seemed best to keep the specimens exposed to the air and at a rather low temperature (3° C to 8° C). After being stained from half an hour to two hours, according to conditions, the material was placed for 20 or 30 minutes in the following freshly made mixture:

ammonium molybdate . . 10 ccm
hydrogen peroxide . . . 2 ccm
hydrochloric acid (strong) . 6 drops

The object in the use of this mixture was to fix the stain in the nervous tissues and to wash it out of all others; but its action in the present case shows that this result does not always follow. The tissues were removed from the mixture as soon as they became greenish, the washing out having by that time gone far enough. This took on an average about half an hour, but the time varied with different specimens. It was best to keep the mixture containing the objects at a low temperature, near 0° C. This solution was then gradually replaced by adding slowly a 1% solution of osmic acid until the ammonium molybdate solution was replaced by a 1% solution of

osmic acid. The tissue was allowed to remain in 1% osmic acid until it became brownish; it was then removed, washed in 50% alcohol, and put into 70% alcohol for twelve hours. After being dehydrated it was imbedded in paraffine, xylol instead of chloroform being used as a solvent. Better preparations were obtained, however, if the thoroughly hardened material were cut free-hand in liver or pith, cleared in xylol, and mounted in balsam.

None of the preparations made by this method, whether imbedded in paraffin or cut free-hand, kept well. Those that were good in June 1896 were of no value a year later, although they had been kept most of the time in the dark, and had never been long exposed to strong light.

Trials with the methylen-blue method did not turn out very successfully until near the end of my work. I was able, however, to get some impregnations, which, though in themselves of little use, were of considerable value when taken in connection with the results obtained by the use of VOM RATH'S method.

It was with VOM RATH'S method that the most satisfactory results were obtained. Although this method does not allow of the isolation of the individual nerve elements, or neurons, it is admirable for tracing nerves, even when they are small and contain but a few fibres. Preparations made by this method are clear and well-defined, although not diagrammatically so, like GOLGI and methylen-blue preparations. They also show the histological structure of ganglionic cells better than either of the former.

By this method fair results were obtained even when special care had not been taken in collecting the material, but the best results were those from material collected in the solution described on page 363. A fair staining of *Moniezia* material was also secured with VOM RATH'S mixture when the worms had been collected in a 2% solution of formaldehyde. Material left in this solution 35 days before being placed in VOM RATH'S fluid gave very fair results. In this case the stain was darker than when fresh material was used, but not too dark to be of considerable value. It is probable that care in regulating the exposure of such material to the action of VOM RATH'S mixture would give a lighter and more desirable stain.

In using VOM RATH'S method fresh material was put into the following VOM RATH'S mixture:

sat. aq. sol. picric acid, filtered . .	500 ccm
glacial acetic acid	3 ccm

platinic chloride (in 5 ccm dist. H_2O) . 5 g
osmic acid crystals . . . . . 2 g

After having remained in this mixture for ten hours the worms were removed and cut into pieces from 1 to 3 cm in length. These were put first into crude pyroligneous acid for from 6 to 10 hours, and then into 70% alcohol for 24 hours. After being dehydrated and inbedded in paraffine they were cut into sections $6^2/_3$ μ thick. This method gave preparations in which the nerves were colored grayish blue, the more highly refractive muscles brown, and the connective tissue pale gray or steel blue.

II. Description of the Nervous System.

A fresh adult specimen of *Moniezia expansa* is commonly about 1 m in length, and from 10 to 15 mm broad at the posterior end. In such an animal there are between 500 and 1000 proglottides. The scolex is on an average 1 mm in diameter and 2 mm in length, measured from the anterior end to a point just posterior to the cephalic ganglion; but the dimensions of the scolex vary considerably in different animals. There are neither rostrum nor hooks in this form. There are two sets of sexual organs in each proglottis, opening one on either margin of the proglottis in a gonopore. The musculature is well developed and is similar to that found in other Taenias.

The anterior part of the excretory system in the scolex of *Moniezia expansa* consists of a horseshoe-shaped tube the curved end of which is situated at about the level of the anterior nerve ring. It lies in the frontal plane and is divided symmetrically by the sagittal plane. Each of the arms of this tube fork, giving rise to branches that pass respectively dorsal and ventral of the cephalic ganglia (Pl. 21, Fig. 1). These branches have been designated as the dextro-dorsal, *va. dx-d*; the dextro-ventral, *va. dx-v*; the sinistro-dorsal, *va. s-d*, and the sinistro-ventral longitudinal excretory tubes (Pl. 21, Figs. 1, 5 and 6). These four tubes bend slightly outward (Pl. 21, Fig. 1), passing close to the surface of the cephalic ganglia, opposite which they turn sharply outward and forward; but, after continuing for a short distance in this direction, they turn backward through an angle of more than 90°, and run parallel to one another and to the lateral nerve. These four excretory tubes pass backward through the neck region into the younger proglottides, the dorsal pair becoming larger and occupying the position of the longitudinal excretory tubes of the

mature proglottides, while the ventral pair becomes smaller and is lost in the older proglottides.

The nervous system of *Moniezia* is imbedded in the connective tissue of the body without any definite bounding membrane or continuous protective structure. Many of the larger and more important trunks, however, have along their courses cells (*cl. vin*) of a peculiar character. They are elliptical, about twice as long and half as thick as they are broad, and from each cell there are given off a number of branching processes that run over the surface of the nerve. I believe that these processes serve to bind the nerve elements into a firmer structure, though they are not very close together, and do not form a continuous covering. These ("binding cells") are shown in Pl. 24, Figs. 15 and 16; Pl. 25, Figs. 29 and 30, and are somewhat different from the Hüllzellen described by ZERNECKE (1895, p. 137) from *Ligula*. They occur upon the nerves of the scolex and upon the large lateral nerve trunks. I have not yet found them upon the other nerves.

1. In the Scolex.

The nervous apparatus of the scolex consists of 1) the anterior nerve ring with its four ganglia; 2) the pair of large cephalic ganglia; 3) the connecting bundles of nerves between 1 and 2 and 4) the dorsal and ventral commissures connecting the outer ends of the cephalic ganglia.

At about one-fifth of the length of the scolex from its anterior end is found that part of the central nervous system which I have called the anterior nerve ring (*n. a*, Pl. 21, Fig. 1). The ring contains four ganglia, one in each of the four quadrants formed by the intersection of the sagittal and lateral planes of the scolex, and a little in front of and deeper than the corresponding acetabulum. These ganglia are here designated according to their positions as the anterior dextro-dorsal (*gn. a. dx-d*, Pl. 21, Fig. 1), sinistro-dorsal (*gn. a. s-d*), dextro-ventral and sinistro-ventral ganglia. The bundles of nerve fibres connecting the ganglia with one another constitute the anterior nerve ring. The ganglia contain a moderate number of ganglionic cells, which differ from those of the rest of the nervous system in size. They are small and, I believe, mostly unipolar, although there are a few bipolar and multipolar ones. These cells (Pl. 24, Figs. 21—24, 26) have a clear and relatively large nucleus, with a deeply staining nucleolus; but no trace of a chromatin network or granular structure was observable in the nucleoplasm. The nuclear

membrane is very thin, often almost indistinguishable from the granular cytoplasm that surrounds the nucleus, but it is not of uniform thickness, small thickenings appearing without regular arrangement upon its inner surface. The cytoplasmic contents are gathered about the nucleus into a dense granular mass, from which threads and films of spongioplasm radiate through the hyaloplasm to the cell wall, thus producing more or less of a stellate appearance (Pl. 24, Figs. 21—24, 26). From these anterior ganglia are given off nerve fibres that are distributed to the anterior end of the scolex, to the acetabula, and to the musculature of that region. I was not able to discover any regularity in the number or distribution of these branches, such as NIEMIEC (1885) has shown; there was instead a very loose, poorly defined, set of nerves that crossed and recrossed one another in a very confusing manner.

NIEMIEC (1885) has described in *Taenia coenurus* a nerve ring lying anterior to the acetabula, but having eight ganglia — instead of four, as in *Moniezia* — placed in pairs, one pair in each quadrant of the scolex. In *Taenia serrata* he also found an anterior nerve ring, but without any pronounced ganglionic enlargements.

In *Moniezia expansa*, as in *Taenia coenurus*, there are eight distinct longitudinal nerve trunks that pass backward from the anterior nerve ring, two arising in each quadrant of the ring, but unlike *Taenia coenurus* these large pairs of nerve trunks have their origin in the posterior surface of each of the four anterior ganglia, one on the external edge of the ganglion, the other on its internal edge. The one arising on the inner edge which is the larger, passes to the cephalic ganglion of its own side, and in passing backward approaches toward the chief axis of the worm; while the one that arises from the outer edge runs posteriorly parallel to the surface, becoming either one of the two dorsal or two ventral longitudinal nerves. (The further description of these outer nerves will be taken up after an account of the inner nerves and of the position of the nervous apparatus immediately connected with them.)

The two inner nerves arising from the ganglia of the right side of the animal converge until they meet at a point not far behind the division of the excretory tube into its dorsal and ventral branches, where they at the same time unite with the right anterior horn of the cephalic ganglion (Pl. 21, Figs. 1 and 2). The nerves of the left side have similar relations. These nerves may be called the cephalic connectives, being simply compact bundles of nerve fibres without

ganglionic cells or any of the protecting or "binding" cells characteristic of other portions of the nervous system. They do not give off branches in any part of their entire length, but are simply connectives between the anterior ganglia and the main portion of the central nervous system — the pair of large cephalic ganglia.

The large cephalic ganglia are situated in the posterior part of the scolex, a little behind the acetabula, one on each side of the sagittal plane. Each of these cephalic ganglia consists of a large rounded mass or body (compare Pl. 21, Figs. 1 and 5, and Pl. 22, Fig. 8) with a fairly smooth even surface and two projections or horns. The anterior median side of each is prolonged anteriorally into a conical process, the anterior horn (Pl. 22, Fig. 8 *conu. a*), which receives the fibres of the cephalic connectives of its own side. The lateral portion of each ganglion is also prolonged into a cone-shaped structure, the external horn (*conu. ex*), which contains the fibres of the lateral nerve. The two ganglia are connected with each other by a relatively small commissure (Pl. 22, Fig. 8 *coms*), the fissure between the ganglia in the median plane being deep, especially in front and behind.

The body of the cephalic ganglion is made up of a core of ganglionic cells traversed by nerve fibres and a cortical portion composed almost entirely of fibres, the whole being enveloped in the richly branched "binding" cells. The ganglionic cells are not as large as those in the ganglia of the proglottides, but they are like them in every other respect. Many of them are multipolar, and are often richly supplied with branching processes (Pl. 24, Fig. 18). The nuclei are relatively large, spherical, hyaline, with a deeply staining nucleolus but no chromatic network; the nuclear membrane is thin, has irregular, thickened places, and in some instances a shrunken appearance, very much like that found by HODGE (1892) in the spinal ganglia of Vertebrates after a day's exercise, or after artificial stimulation. In the cell shown in Pl. 24, Fig. 18 the dendritic or protoplasmic processes are very numerous, but in VOM RATH preparations they are not easily followed. Some of the nerve processes of such ganglionic cells have deeply staining thickenings occurring at about equal intervals, as may be seen in some of the processes of Fig. 18. Bipolar cells are much more common than those of the unipolar type, and occasionally there is found a peculiar form (Pl. 24, Fig. 19), which might readily be taken for a unipolar cell, but which is in reality bipolar. The cytoplasmic contents of these cells have the same stellate arrangement

as in the other ganglionic cells of this animal. Where the nerve fibre joins the cell there is an accumulation of granules similar to that about the nucleus (Pl. 24, Fig. 18). The anterior and external horns of the cephalic ganglia have but few ganglionic cells, being for the most part composed of nerve fibres.

Although I am not yet prepared to give a detailed account of the path taken by the nerve fibres through the cephalic ganglion, I have to some extent followed their courses and give what I believe to be the paths of the principal groups of them. There is a large bundle of fibres (Pl. 22, Fig. 8 *B*), which seems to arise from the central ganglionic mass of either side, and to pass through the posterior part of the transverse commissure into the ganglion of the opposite side. The bundle here traverses the posterior part of the ganglion, curving around behind the ganglionic core, and emerges through the external horn to enter the lateral nerve of the side opposite that in which it arose. This bundle is joined just before it passes through the transverse commissure, by a smaller bundle (Pl. 22, Fig. 8 *D*), which enters the cephalic ganglion through its anterior horn, probably arising from the two "anterior ganglia" of the same side of the scolex. A third bundle of fibres arising from the anterior ganglia of each side enters the cephalic ganglion of the same side through its anterior horn, passes along the anterior border of this ganglion near its surface and finally emerges through its external horn to enter the lateral nerve of the same side of the scolex in which it originated. There are also several other smaller distinct bundles of nerve fibres in the body of the cephalic ganglia, the most conspicuous one being a bundle that traverses the anterior part of the transverse commissure connecting the central ganglionic cells of one cephalic ganglion with those of the other.

The external horn of the cephalic ganglion is enlarged where it joins the lateral nerve, and from this enlargement arise several small nerves that are distributed to the acetabula and to the muscles that operate them. From this enlargement there also arise two broad bands of nervous tissue, one from its dorsal, the other from its ventral surface. The former passes dorsad of the dorsal excretory tubes, the latter ventrad of the ventral excretory tubes, to enter the corresponding regions of the cephalic ganglion of the opposite side of the body. These are respectively the dorsal and ventral cephalic commissures (Pl. 21, Figs. 1 and 5 *coms.d'*, *coms.v'*). These commissures are thin bands of loosely arranged nerve fibres, which in

their course meet the two dorsal and two ventral longitudinal nerves. Not only do fibres of these bands decussate with those of the longitudinal nerves, but fibres also pass from commissure to longitudinal nerve and vice versa. Along the course of these commissures there are found a few ganglionic cells which are mostly of the unipolar type (Pl. 22, Fig. 11). The position and appearance of these commissures reminds one of the two hexagonal commissures found by NIEMIEC (1885) in *Taenia coenurus* and *T. serrata,* with one of which they are probably homologous, although apparently they are less well defined nerves than those in the species studied by NIEMIEC.

Returning to the four outer nerves arising from the anterior ganglia, it is found that in running backward they approach one another slightly and that each passes through the dorsal or ventral cephalic commissure, from which a few nerve fibres are received. Behind the cephalic commissure they run nearly parallel with one another, becoming the dextro-dorsal, sinistro-dorsal, dextro-ventral and sinistro-ventral longitudinal nerves (Pl. 21, Figs. 1, 2, 4 and 5). In the scolex these are simple, rather compact bundles of nerves, without ganglionic or "binding" cells; but in passing backward ganglionic cells begin to appear in the neck region. At first these are few, but as older proglottides are reached the number increases. These nerves correspond exactly in origin, position and the course taken with those described by NIEMIEC (1885) in *Taenia coenurus* and *T. serrata.* NIEMIEC was unable to trace them beyond the neck region, but I have found them in proglottides taken from all parts of the worm, and always occupying the same relative position in the proglottis. Although I have not traced them continuously from proglottis to proglottis through an entire strobila, I think that their occurrence in the same relative position in proglottides taken at random in the same animal is evidence enough that they are continuous throughout the entire length of the worm.

2. In the Neck Region.

In the neck region of *Monieza* the most prominent nerves are the six longitudinal ones. The two large lateral nerves arising from the external horns of the cephalic ganglia lie in the usual position external to the longitudinal excretory tube. They are single nerve trunks nearly circular in cross-section, and not sharply defined in outline. I have not succeeded in finding in *Moniezia* the two accessory lateral nerves which are described for other forms by NIEMIEC,

LÜHE and COHN, as accompanying each of the lateral nerve trunks. For the first 5 mm behind the scolex the lateral nerves are of uniform diameter, they possess only a few ganglionic cells and no trace of ganglionic enlargements. The "binding" cells enveloping them are few, long tracts existing without any such elements. The branches arising from the lateral nerves are mostly limited to the formation of the dorsal and ventral commissures (Pl. 21, Fig. 1).

The dorsal and ventral nerves are likewise without ganglionic enlargements in the neck region, and the ganglionic cells are few. In the posterior part of the neck region where the proglottides begin to be distinguishable, the nerves begin to assume the condition which they present in the mature segments. In this portion of the neck region each lateral nerve begins to exhibit an enlargement at a point near the posterior margin of the proglottis. This enlargement is due to the increased number of ganglionic cells occurring in the nerve at that point; these increase in number continuously until the proglottis is mature. The enlargement of the lateral nerve caused by this increase in the number and size of the ganglionic cells is the first indication of the posterior lateral ganglion (Pl. 21, Fig. 1 *gn. l. p*). The position of these ganglia is indicated in the preceding portion of the neck region by the presence of the small branches from the lateral nerve which correspond in position to the posterior part of each young proglottis. These branches are undoubtedly the beginnings of the dorsal and ventral commissures of the mature segments which are recognizable, then, before the ganglionic enlargements of the lateral nerve with which they are connected.

At a distance of 30 mm from the scolex the posterior lateral ganglia are well marked. In favorable sections from this region made in a frontal plane it is possible to trace the individual neurons of the lateral nerves (Pl. 26, Fig. 32). The ganglionic cells are usually nearly triangular and of the unipolar type; there are a great number of dendritic, or protoplasmic, processes which interlace with those of neighboring ganglionic cells. In the section shown in Pl. 26, Fig. 32, there are three unipolar and two bipolar ganglionic cells, which, for some reason, are more deeply stained than the others. At least two kinds of neurons are distinguishable; in one the ganglionic cell sends a nerve fibre posteriorly from its ganglion to the next following one; in the other anteriorly to the preceding ganglion. A complete isolated neuron is shown in Pl. 24, Fig. 25.

In each of the ganglionic enlargements there lie between the

ganglionic cells others which do not appear to have any nerve fibre connected with them. These cells are richly branched, the branches interlacing with the dentritic processes of the ganglionic cells. It is impossible to say whether they act as a means of connection between different neurons, whether they are developing ganglionic cells, or have some other function. One of these cells is shown very faintly in Pl. 26, Fig. 32. In this region the dorsal and ventral commissures have become in so far complete that they can be traced from the posterior lateral ganglion of one side to that of the other. The ganglia of the dorsal and ventral nerves have also begun to be distinguishable, but there is as yet no trace of the anterior lateral ganglion, nor of the genital or marginal nerves. At least it has not been possible by any method which I have used to demonstrate their presence until after the dorsal and ventral commissures, as well as the dorsal and ventral ganglia, have made their appearance.

3. In the Mature Proglottis.

In each lateral half of every proglottis there is, besides the dorsal and the ventral commissures and the large lateral nerve, a dorsal and a ventral longitudinal nerve, an internal and an external genital nerve, and a marginal nerve. The lateral nerve trunk is imbedded in the parenchyma of the body, from which it is not sharply defined; it is elliptical in cross-section, the larger axis of the ellipse having a dorso-ventral direction. The course of these nerves is nearly parallel to that of the longitudinal excretory tube (Pl. 22, Fig. 6 *n.l*). The nerve is a compact bundle of naked axis cylinders separated from one another by a structureless hyaline matrix, the whole being bound together by peculiar binding or protecting cells like those found in the scolex. These cells appear elliptical in outline, and send out a considerable number of branching processes that run over the surface of the nerve, and serve, I believe, to bind the nerve fibres into a compact bundle and to separate them in a measure from the tissues in which the nerve is imbedded (Pl. 25, Fig. 30 *cl.vin*). These branches are not, however, so numerous nor so dendritic in character as in the cells of similar function figured by ZERNECKE (1896, tab. 13, figs. 55, 56) for *Ligula*. In longitudinal sections of the nerve they appear lenticular, the edges being prolonged for a considerable distance over the surface of the nerve trunk. In some regions they lie singly, separated from each other by a considerable distance; in others they lie close together, as seen in Figs. 9 (Pl. 22) and 15 (Pl. 24). There seems to be no

regularity as to their arrangement. In Vom Rath preparations the nuclei of some of these cells are deeply stained and each contains a very dense nucleolus (*vin. cl*, Pl. 25, Fig. 29 and Pl. 24, Fig. 15); whereas, in other binding cells of the same preparation the nucleus is unstained, while the nucleolus is deeply stained. Granular cytoplasm is usually collected around the nucleus and passes thence in radiating and sometimes branching strands to the periphery of the cell, giving the whole a stellate appearance. These are probably modified mesodermal cells.

Along the course of the lateral nerve between the anterior and posterior lateral ganglia there are ganglionic cells, some of them in the nerve itself others outside the nerve. These ganglionic cells are mostly bipolar or multipolar, but in one case (Pl. 25, Fig. 30 *cl. gn*), two unipolar ganglionic cells were found lying outside the nerve and sending each an axis cylinder into the nerve. In one case the fibre shortly left the nerve, and, passing outward, terminated in a cup-shaped structure, which enveloped one end of an ellipsoidal, hyaline, structureless body, the other end of which was enveloped by a similar cup-shaped structure formed by the end of another nerve. I have observed this structure in several methylen-blue preparations, however I am inclined to believe that it is due to some post-mortem change caused by the reagents used. The ganglionic cells which lie in the nerve substance (Pl. 24, Fig. 15 *cl. gn*) are usually small and of the multipolar type, and are frequently seen to give rise to nerve fibres which emerge from the nerve.

The lateral nerve is single throughout its entire length, and no trace of additional lateral nerves, such as have been described in other Cestodes, has been found.

In the posterior part of each proglottis the lateral nerve becomes enlarged by the aggregation of ganglionic cells, forming what I have called the posterior lateral ganglion (Pl. 22, Fig. 6 *gn. l. p*). It lies close to the longitudinal excretory tube (Pl. 25, Fig. 28 and Pl. 26, Fig. 31), and nearly opposite the point whence the transverse excretory tube is given off. The ganglion is ellipsoidal, its antero-posterior diameter being greater than its dorso-ventral diameter, which, in turn, is greater than its dextro-sinistral diameter. It varies considerably in size, being largest in those proglottides which contain very young embryos while in the older proglottides it undergoes degeneration.

From this ganglion there arise besides several smaller nerves, two large ones, one from its dorsal, the other from its ventral surface;

these pass mediad, one above, the other below the excretory tube, crossing the proglottis to the corresponding regions of the ganglion of the opposite side. These two nerves are the dorsal and the ventral commissures (Pl. 22, Figs. 6 and 7 *coms. d* and *coms. v*). They are loose, band-like nerves flattened dorso-ventrally, and plentifully supplied with ganglionic cells, either singly or in groups, at points where nerves are given off. The ganglionic cells are almost always of the bipolar type (Pl. 24, Fig. 20), but otherwise have the same characteristics as the ganglionic cells from the other parts of the nervous system. I have not found any binding cells along the dorsal commissure, and from its loose texture it is doubtful if any exist. This nerve in its passage across the proglottis lies slightly behind the transverse excretory tube and among the transverse muscles, some of which frequently run through the substance of the nerve. Because of this peculiarity the nerve is often so broken up and concealed by the bundles of muscles that it is difficult to trace its course. In places it appears as a moderately compact nerve, but it may shortly become a mere tangle of nerve and muscle fibres, from which it may emerge as a broad sheet of nervous tissue. This nerve is inconstant in form, like all the nerve structures excepting those of the scolex and the lateral nerves. Its inconstancy of form is due, I believe, to the fact that the nerve elements lie embedded in the tissues of the body without any protective structure to bind them into a compact nerve.

From the outer edge of the posterior lateral ganglion there arises a cluster of nerve fibres, the largest and most important of which is the marginal nerve (*n. marg*). This arises from the anterior portion of the outer edge of the ganglion, passes outward and then anteriad through the greater part of the margin of the proglottis (Pl. 22, Fig. 6, Pl. 23, Fig. 12). A short thick nerve arises from the posterior outer edge of the ganglion, and passes posteriad into the proglottis, which lies immediately behind that in which the ganglion is located. A cluster of still shorter branching nerves arises from the lateral margin of the ganglion between the marginal and the posterior nerves and is distributed to the outer posterior angle of the proglottis.

The posterior lateral ganglion is made up of a mass of ganglionic cells and a great number of nerve fibres intermingled in a most confusing manner. Transverse sections of the proglottis in the plane of the dorsal and ventral commissures (Pl. 25, Fig. 28 and Pl. 26, Fig. 31) are the most instructive, although frontal sections

(Pl. 21, Fig. 3), are nearly as good. The nerve fibres, on passing into and out of the ganglion, pursue almost every possible direction, making a tangle that I have not been able to unravel; yet there appear to be certain paths within the ganglion that are recognizable, owing to the number of nerve fibres which take the same direction. The ganglionic cells associated with the nerve fibres appear in Fig. 28 (Pl. 25) and Fig. 31 (Pl. 26) to be of a rounded form, but they are in reality multipolar, since they each possess numerous protoplasmic processes. Isolated cells from this ganglion are shown in Figs. 16 and 17 (Pl. 24) more highly magnified. Two kinds of these nerve cells may perhaps be recognized, differing in size and in the richness of their branching; those which lie in the center of the ganglion are larger and more richly branched, while those at the periphery are smaller, usually bipolar, and less richly branched. Otherwise the cells are alike. The nucleus is rather small, compared with the nucleus of a ganglionic cell of the scolex, and hyaline, and it contains a deeply staining nucleolus. In some cases under a very high magnification a faint chromatic reticulum may be seen in the nucleus. The nuclear membrane is very thin, with no observed thickenings, and shows no such wrinkles as are often seen in the scolex. The coarsely granular cytoplasm is gathered into a mass about the nucleus, from which films and threads of similar appearance radiate through the more finely granular cytoplasm that occupies the periphery of the cell. Therefore these cells invariably have a stellate appearance.

There are also ganglionic cells that lie just outside the ganglion and send their nerve fibres for the most part into the ganglion. These cells are usually multipolar, possessing a few dendritic processes. The nucleus is small, with a large, deeply-staining nucleolus (Pl. 24, Fig. 16), and very frequently a well developed chromatic reticulum. The cytoplasmic contents present the usual stellate appearance. I have not yet found in the posterior lateral ganglion of the mature proglottides any of the richly branched binding cells found in the younger proglottides. Either they are not present (which I can hardly believe), or, more likely, Vom Rath's method will not differentiate them sufficiently in the mature specimens.

Upon the lateral nerve, at about the point where it crosses the sexual ducts in their passage to the gonopore, there is another ganglionic enlargement — the anterior lateral ganglion (*gn.l.a*, Pl. 22, Fig. 6, Pl. 23, Fig. 12). This is a dorsal enlargement of the lateral nerve due to the accumulation of ganglionic cells at that point (Pl. 26,

Fig. 33), as in the case of the larger posterior lateral ganglion. In structure it is like the posterior lateral ganglion, being composed of a number of ganglionic cells embedded in a matrix of nerve fibres, and the ganglionic cells are in every respect like those of the posterior lateral ganglion. From the dorsal surface of the anterior ganglion there arise, sometimes as a single trunk, two nerves which pass medianward and dorsad and soon divide. One nerve passes laterad, becoming the external genital nerve (*n.gen.ex*), and is distributed to the region of the gonopore; the other passes inward, becomes the internal genital nerve (*n.gen.i*, Pl. 22, Fig. 6; Pl. 23, Fig. 12; Pl. 26, Fig. 33; Pl. 24, Fig. 27), and is distributed to the ovaries, uterus, and other sexual organs of the region. There are a few ganglionic cells along the course of these nerves, but no binding cells. As far as I was able to discover the anterior lateral ganglion does not become apparent until the proglottis is nearly mature, although the two nerves are found in younger proglottides. This is due probably to the increased activity of those parts upon reaching sexual maturity.

There is a ventral commissure (Pl. 22, Figs. 6 and 7 *coms.v*), connecting the ventral surfaces of the posterior lateral ganglia of each proglottis, and corresponding in size, shape and relations to the dorsal commissure. These two commissures, together with the posterior lateral ganglia, form a complete nerve ring, embracing the two longitudinal excretory tubes, and uniting the lateral nerve of one side with its fellow of the opposite side. These two commissural nerves are united to each other by means of two dorso-ventral connectives. These connectives have the form of a loose band of nerve fibres that passes dorso-ventrally from one commissure to the other close to the median surface of the longitudinal excretory tube, and just behind the union of the longitudinal and transverse excretory tubes (*con't.d-v*, Pl. 22, Figs. 6, 7; Pl. 25, Fig. 28; Pl. 26, Fig. 31). One of these connectives with a small part of each of two commissures and the corresponding posterior lateral ganglion forms a complete ring of nerve tissue that encircles the longitudinal excretory tube immediately behind the transverse excretory tube. This dorso-ventral connective is like the commissures in structure, being a band of loosely united nerve fibres associated with a greater or less number of ganglionic cells. A few nerve fibres are seen to pass off from these connectives, but I have not been able to trace them to their terminations.

The marginal nerve (Pl. 22, Fig. 6 *n.marg*), arises from the an-

terior outer edge of the posterior lateral ganglion, passes outward for a short distance, and then turning passes forward through about three-fourths of the length of the proglottis; but in no examples that I have seen is it continuous through the whole of the proglottis, as stated by COHN (1897) for *Taenia*. In my preparations the branches of the marginal nerve are distributed to the margin of the posterior three-fourths of the proglottis (Pl. 23, Fig. 12), only a few fibres indeed reaching as far forward as the anterior fourth. The fibres from the short, posteriorly directed marginal nerve ennervate the greater part of the margin of the anterior fourth of the next following proglottis, but I was not able to find any branches that extended far enough backward to meet the fibres of the long marginal nerve. It is of course possible, in view of the great variability of the peripheral nerves of the parasites, that there may be cases where the marginal nerve is continuous and well-marked throughout the entire length of the proglottis, but I have not yet seen such a case. The structure of the marginal nerve is shown in Pl. 22, Fig. 10. Nerve fibres are given off on all its sides and at frequent intervals, and there are numerous, spindle-shaped ganglionic cells along its course.

The two dorsal and two ventral nerves discovered by NIEMIEC in the scolex and neck region of *Taenia*, are easily demonstrated in the younger proglottides (Pl. 21, Fig. 1), and in some cases, at least, exist in the mature proglottides as well-defined nerves with the elements closely gathered together. These, which I have described and figured in an earlier paper, are also represented in the diagrammatic Figs. 1 (Pl. 21), 6, 7 (Pl. 22), 12 and 13 (Pl. 23). It must not be supposed, however, that these nerves always appear with the same diagrammatic clearness, for it is only in exceptional cases that they are so well defined. In the greater number of specimens examined these nerves had become a loose, ill-defined band of tissue lying in the layer of the longitudinal muscles, with which the nerve is closely associated. In my earlier paper I have called these nerves dorsal and ventral connectives, but I am now satisfied that they are continuous throughout the entire length of the animal, and are therefore equivalent to the four nerves of NIEMIEC. These nerves pass through, or are closely associated with, the dorsal and ventral commissures of each proglottis. At the place of crossing the two form a loose mass of nerve fibres with an increased number of ganglionic cells. These crossings I have previously designated as ganglia, and have named them according to their position in the proglottis. I have continued that nomenclature in the

present paper, though it may be an open question whether the slight accumulation of ganglionic cells in these regions warrants giving them the dignity of ganglia. However, in those cases where the nerve elements are compacted, these ganglia present a structure not unlike that of the other ganglia of the nervous system.

The dorsal and ventral longitudinal nerves give off lateral branches along their entire length, which lie in the layer of the longitudinal muscles. Fig. 14 (Pl. 23) shows one of these nerves (the right dorsal) which is more compact than usual. In the region of the two branches there are ganglionic cells.

It gives me pleasure to acknowledge my indebtedness to the director of the Zoological Laboratory, Dr. E. L. MARK, for his kindly critericism and many helpful suggestions given me during the progress of my work.

Cambridge, Mass., Sept. 1, 1897.

Postscript. Since this paper was written COHN (in: Zool. Jahrb., V. 12, Anat., 1899, p. 425—76), has published his studies on the nervous system of several Cestodes. He believes that all of the longitudinal nerves, together with their transverse connections in both scolex and proglottides, constitute the central nervous system. The branches from these to the various organs and to the surface of the animal he regards as the peripheral system.

From the conditions that I have found in *Moniezia* I believe this division to be justifiable, and that there is a true central nervous system in Cestodes. I do not, however, agree with COHN's view that the "main commissure" is a mere connective. I find in *Moniezia* that there is a well developed pair of central ganglia in the scolex. These ganglia possess ganglionic cells which send nerve fibres to other parts of the nervous system of the scolex, and posteriorly to the proglottides.

Since this paper was written I have studied further the nervous system of Cestodes, using with some success methylen-blue and GOLGI impregnations. I find a distinct central system in the scolex, which I think may function as a central coördinating center — a brain. The rest of the central nervous system is comparable to a longitudinal nerve chain. The conclusions reached in this paper as to the paths taken by the fibres in the cephalic ganglion were substantiated by my more recent methylen-blue and GOLGI preparations.

Unfortunately all my drawings and preparations were lost in a fire which occurred in March 1898, and I have not since been able to return to the subject.

Cambridge, Mass., U.S.A., Dec. 14, 1899.

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Explanation of Plates.

Plate 21—26.

Abbreviations.

a anterior
act acetabulum
cl. gn ganglionic cell
cl. vin binding cell
co body of cephalic ganglion
coms commissure of cephalic ganglion
coms. d dorsal commissure of proglottis
coms. d' dorsal cephalic commissure
coms. v ventral commissure of proglottis
coms. v' ventral cephalic commissure
con't. cep. dx right connective between the cephalic and the anterior ganglia
con't. d-v dorso-ventral connective
conu. a anterior horn of cephalic ganglion
conu. ex external horn of cephalic ganglion
cta cuticula
d dorsal
gn. a. dx-d anterior dextro-dorsal ganglion
gn. a. s-v anterior sinistro-ventral ganglion
gn. dx right cephalic ganglion
gn. dx-d dextro-dorsal ganglion
gn. dx-v dextro-ventral ganglion
gn. l. a anterior lateral ganglion
gn. l. p posterior lateral ganglion
gn. s left cephalic ganglion
gn. s-d sinistro-dorsal ganglion
gn. s-v sinistro-ventral ganglion
n. a anterior nerve ring
n. gen. ex external genital nerve
n. gen. i internal genital nerve
n. l lateral nerve
n. lg. dx-d dextro-dorsal longitudinal nerve
n. lg. dx-v dextro-ventral longitudinal nerve
n. lg. s-d sinistro-dorsal longitudinal nerve
n. lg. s-v sinistro-ventral longitudinal nerve
n. marg marginal nerve
p posterior
ut uterus
v ventral
va. dx right arm of the anterior loop of excretory tube in scolex
va. dx-d dextro-dorsal longitudinal excretory tube
va. dx-v dextro-ventral longitudinal excretory tube
va. lg longitudinal excretory tube
va. s-d sinistro-dorsal longitudinal excretory tube
va. s-v sinistro-ventral longitudinal excretory tube.
va. t transverse excretory tube

Plate 21.

Figs. 1, 2, 4 and 5 are diagrammatic.

Fig. 1. Reconstruction of the nervous system in the scolex of *Moniezia expansa.*

Fig. 2. Transverse section of the scolex at the region $\beta\beta'$ (Fig. 1), showing the position of the nerve structures.

Fig. 3. Frontal section through the posterior lateral ganglion. From a Vom Rath preparation. × 500.

Fig. 4. Transverse section of the scolex at the region $\alpha\alpha'$ (Fig. 1), showing the position of the nerve structures etc. (*n. l. dx-d* should be *n. lg. dx-d*).

Fig. 5. Transverse section of the scolex at the region $\gamma\gamma'$ (Fig. 1), showing the position of the nerve structures, etc. at that level.

Plate 22.

Fig. 6. Diagrammatic reconstruction of the nervous system in four proglottides.

Fig. 7. Transverse section of a proglottis through the posterior lateral ganglion (diagrammatic).

Fig. 8. Diagrammatic representation of the paths taken by the nerve fibres that enter and leave the cephalic ganglia (see p. 371).

Fig. 9. Parasagittal section through the longitudinal nerve in a region between the posterior and anterior lateral ganglia, showing "binding" cells and ganglionic cells lying along the nerve. From a Vom Rath preparation. × 500. (*vt* by mistake for *ut.*)

Fig. 10. Parasagittal section of the marginal nerve, showing nerve fibres passing off from it. Vom Rath preparation. × 1100.

Fig. 11. Section (transverse to the chief axis of the scolex), through the dorsal cephalic commissure, showing bipolar ganglionic cells.

Plate 23.

Fig. 12. Portion of a diagrammatic transverse section of a proglottis through the anterior lateral ganglion and the genital nerves, showing the distribution of the nerve fibres from the marginal nerve, and from the sinistro-dorsal and the sinistro-ventral longitudinal nerves.

Fig. 13. Parasagittal section (diagrammatic), of a proglottis through the sinistro-dorsal and the sinistro-ventral longitudinal nerves, showing distribution of the nerve fibres.

Fig. 14. Portion of a frontal section of a proglottis through a branch of the dextro-dorsal longitudinal nerve. Vom Rath's preparation. × 1000.

Plate 24.

Fig. 15. A frontal section of the lateral nerve showing ganglionic and binding cells. Vom Rath. × 700.

Fig. 16. Portion of a transverse section of a posterior lateral ganglion, showing protecting ("binding") cells upon the surface of the

ganglion and two ganglionic cells that send nerve fibres (in another plane) into the ganglion. VOM RATH preparation. × 1500.

Fig. 17. A bipolar ganglionic cell from the posterior lateral ganglion. VOM RATH. × 1450.

Fig. 18. A multipolar ganglionic cell from the cephalic ganglion. VOM RATH. × 1500.

Fig. 19. A bipolar ganglionic cell from the cephalic ganglion. VOM RATH. × 1450.

Fig. 20. A bipolar ganglionic cell from the posterior lateral ganglion. VOM RATH. × 1450.

Figs. 21 and 22. Unipolar ganglionic cells from the anterior ganglia. VOM RATH. × 1450.

Figs. 23 and 24. Bipolar ganglionic cells from the anterior ganglia. VOM RATH. × 1450.

Fig. 25. A neuron from the lateral nerve in the neck region. VOM RATH. × 1500.

Fig. 26. A unipolar ganglionic cell from the anterior dorso-dextral ganglion. VOM RATH. × 1450.

Fig. 27. Frontal section of the anterior lateral ganglion and genital nerves. VOM RATH. × 700.

Plate 25.

Fig. 28. Transverse section through the posterior lateral ganglion. VOM RATH. × 800.

Fig. 29. Protecting cell as seen on lateral nerve. VOM RATH. × 800.

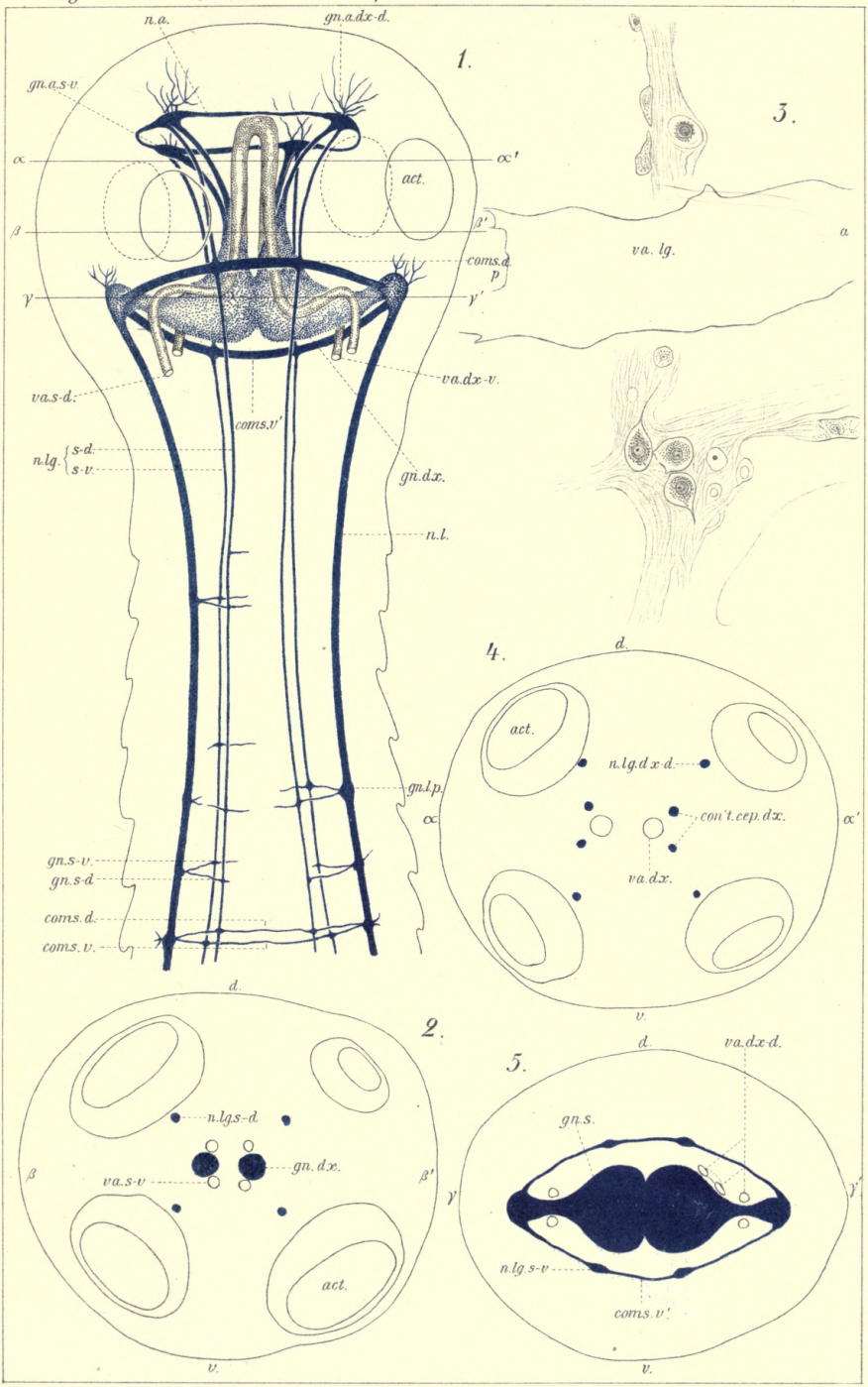
Fig. 30. Dorso-ventral longitudinal section through lateral nerve showing protecting and ganglionic cells. VOM RATH. × 1000.

Plate 26.

Fig. 31. Transverse section of the posterior lateral ganglion. VOM RATH. × 800.

Fig. 32. Frontal section of the posterior lateral ganglion in the "neck" region. VOM RATH. × 900.

Fig. 33. Frontal section through the anterior lateral ganglion. VOM RATH. × 800.


1.
n.a.
gn.a.dx-d.
gn.a.s-v.
∝
∝'
act.
β
β'
coms.d.
p
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va.dx-v.
va.s-d.
coms.v'
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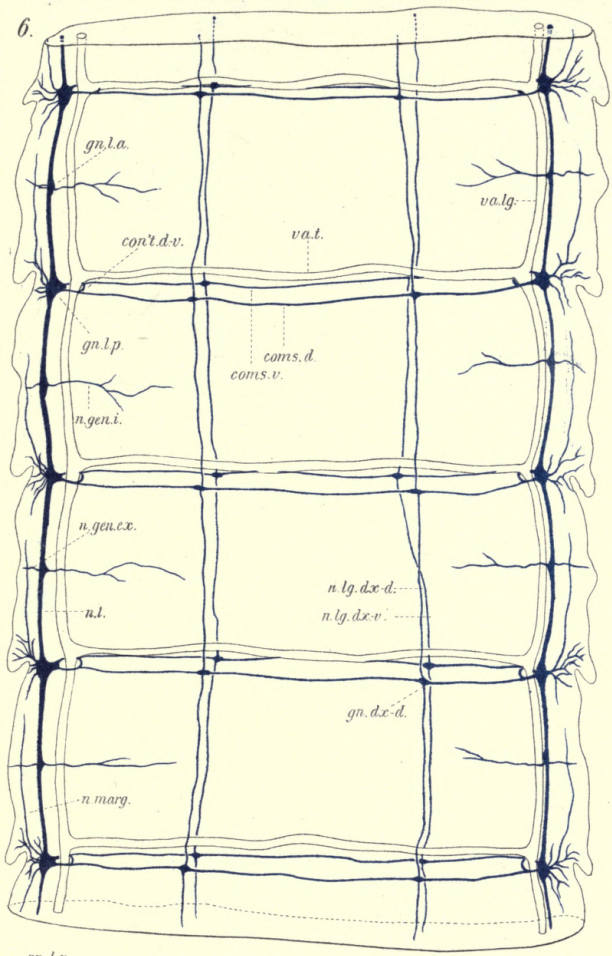
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gn.l.a.
va.lg.
con't.d.v.
va.t.
gn.l.p.
coms.d.
coms.v.
n.gen.i.
n.gen.ex.
n.l.
n.lg.dx-d.
n.lg.dx-v.
gn.dx-d.
n.marg.
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gn.dx-d.
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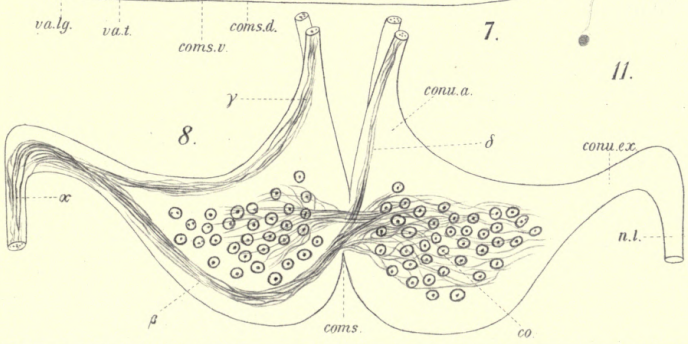
9.
vt.
vt.


10.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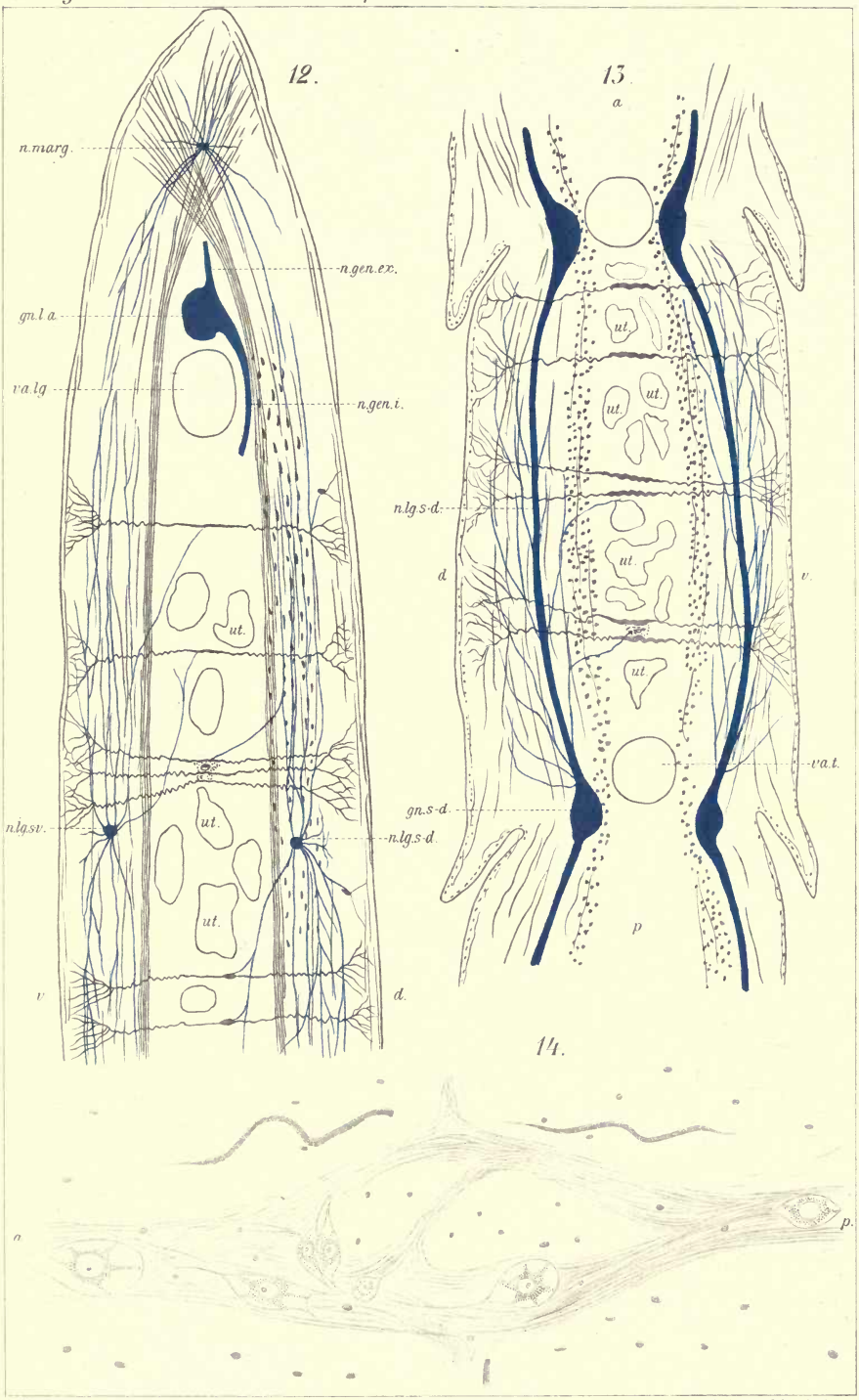
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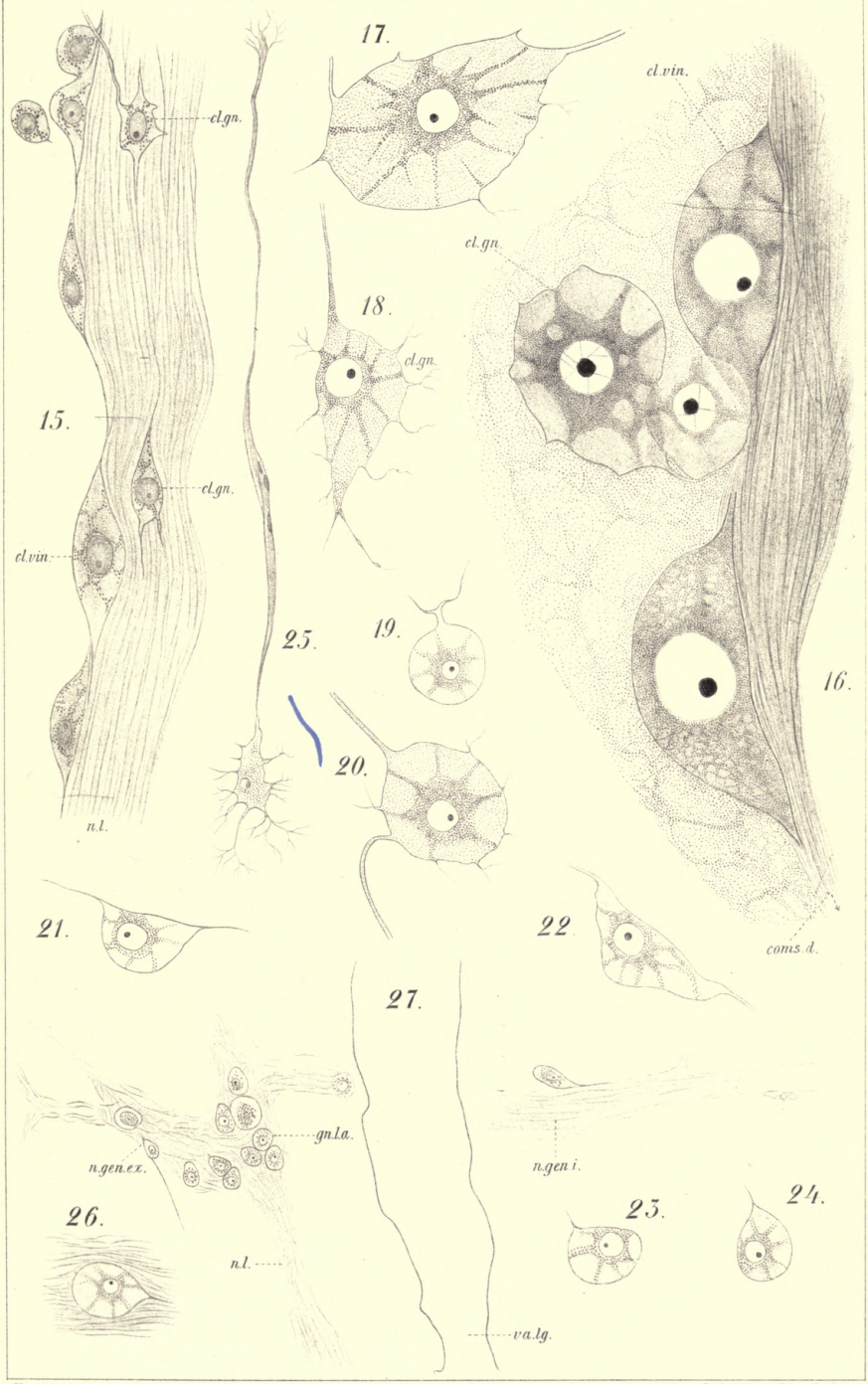
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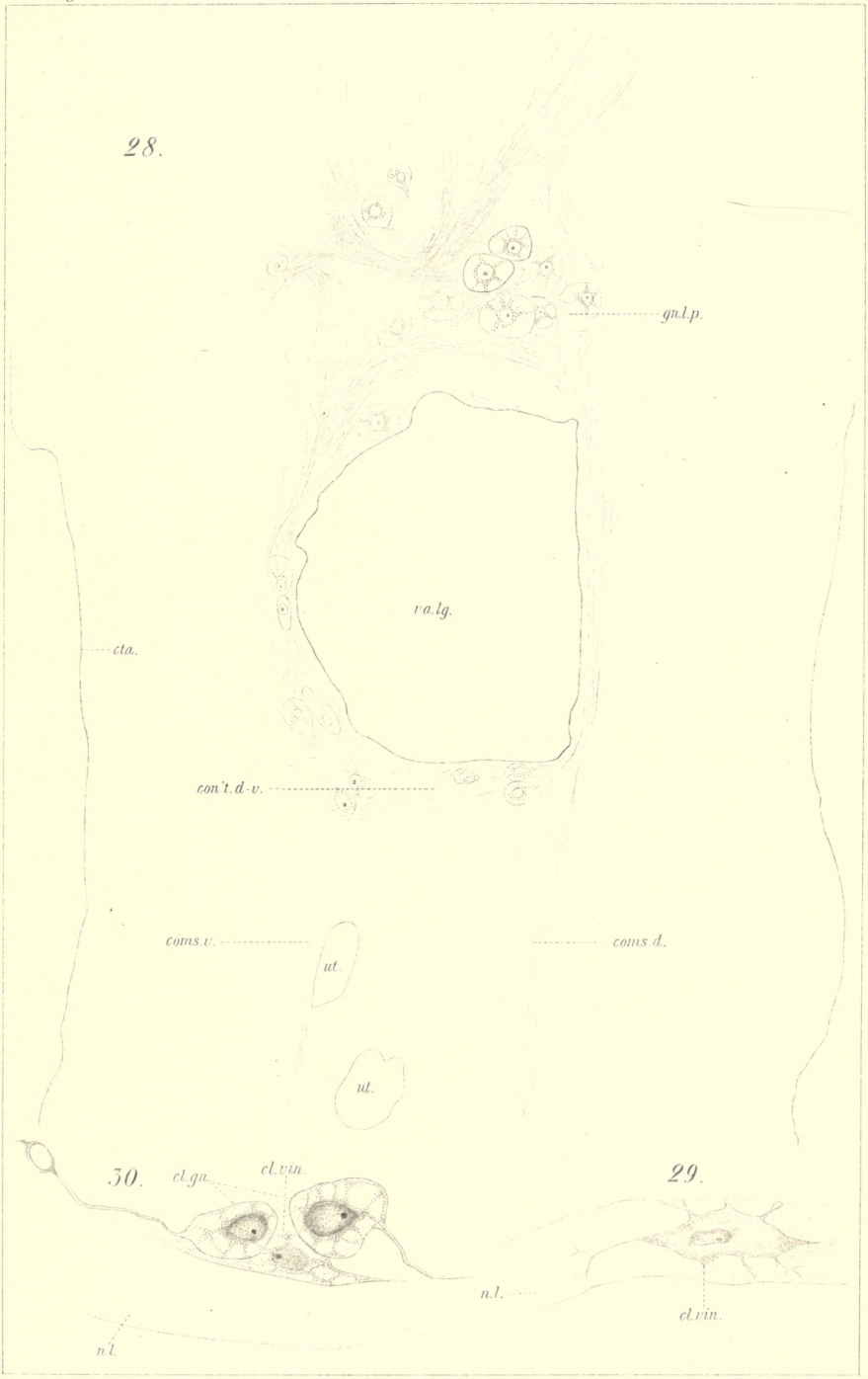
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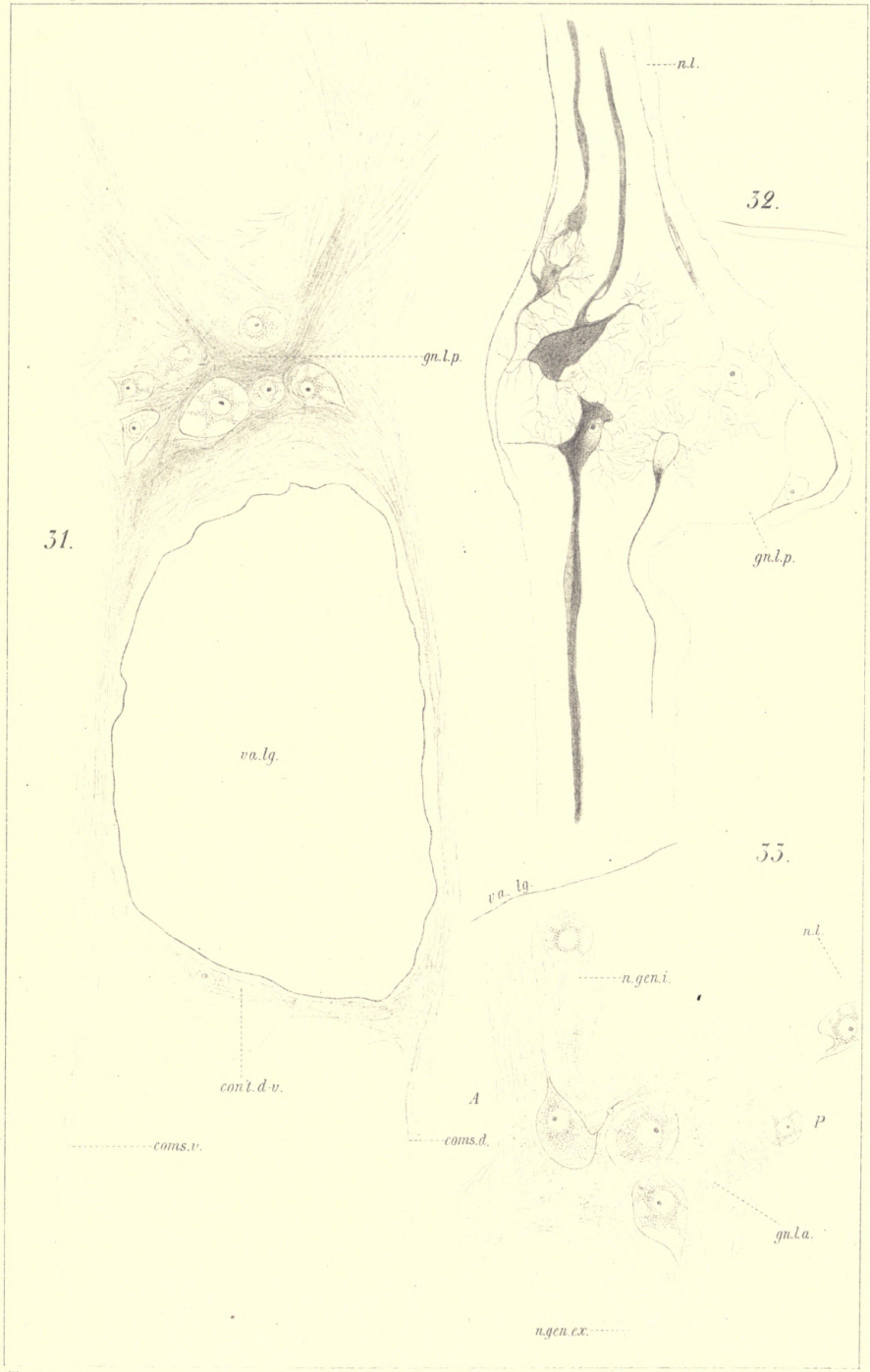
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E. L. MARK, *Director*.

*** Abbreviations used:—

B. M. C. Z. . . . . for Bull. Mus. Comp. Zoöl.
P. A. A. . . . . for Proceed. Amer. Acad. Arts and Sci.
P. B. S. N. H. . . . . for Proceed. Bost. Soc. Nat. Hist.

1. BARNES, W. — On the Development of the Posterior Fissure of the Spinal Cord, and the Reduction of the Central Canal, in the Pig. P. A. A. **19**: 97–110. 3 pls. 1884.

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3. AYERS, H. — On the Development of Oecanthus niveus and its Parasite, Teleas. Mem. Bost. Soc. Nat. Hist. **3**: 225–281. 8 pls. Jan., 1884.

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7. FAXON, W. — Descriptions of New Species of Cambarus; to which is added a Synonymical List of the Known Species of Cambarus and Astacus. P. A. A. **20**: 107–158. Dec., 1884.

8. LOCY, W. — Observations on the Development of Agelena naevia. B. M. C. Z. **12**: 63–103. 12 pls. Jan., 1886.

9. FEWKES, J. W. — Report on the Medusae collected by the U. S. Fish Commission Steamer Albatross in the Region of the Gulf Stream in 1883-'84. Ann. Rep. Comnr. Fish and Fisheries for 1884, 927–980, 10 pls., 1886.

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45. Miller, Gerrit S., Jr. — On the Introitus Vaginæ of certain Muridæ. P. B. S. N. H. **26**: 459–468. 1 pl. Feb., 1895.

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